



Thermal tolerance and preference of exploited turbinid snails near their range limit in a global warming hotspot



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ABSTRACT

Predicted global climate change has prompted numerous studies of thermal tolerances of marine species. The upper thermal tolerance is unknown for most marine species, but will determine their vulnerability to ocean warming. Gastropods in the family Turbinidae are widely harvested for human consumption. To investigate the responses of turbinid snails to future conditions we determined critical thermal maxima (CTMax) and preferred temperatures of *Turbo militaris* and *Lunella undulata* from the tropical-temperate overlap region of northern New South Wales, on the Australian east coast. CTMax were determined at two warming rates: 1 °C/30 min and 1 °C/12 h. The number of snails that lost attachment to the tank wall was recorded at each temperature increment. At the faster rate, *T. militaris* had a significantly higher CTMax (34.0 °C) than *L. undulata* (32.2 °C). At the slower rate the mean of both species was lower and there was no significant difference between them (29.4 °C for *T. militaris* and 29.6 °C for *L. undulata*). This is consistent with differences in thermal inertia possibly allowing animals to tolerate short periods at higher temperatures than is possible during longer exposure times, but other mechanisms are not discounted. The thermoregulatory behaviour of the turban snails was determined in a horizontal thermal gradient. Both species actively sought out particular temperatures along the gradient, suggesting that behavioural responses may be important in ameliorating short-term temperature changes. The preferred temperatures of both species were higher at night (24.0 °C and 26.0 °C) than during the day (22.0 °C and 23.9 °C). As the snails approached their preferred temperature, net hourly displacement decreased. Preferred temperatures were within the average seasonal seawater temperature range in this region. However, with future predicted water temperature trends, the species could experience increased periods of thermal stress, possibly exceeding CTMax and potentially leading to range contractions.

1. Introduction

Ocean warming has been identified as one of the main threats to marine organisms. Globally, it is estimated that by the end of 21st century, the ocean temperature will have increased by 2.0–4.5 °C (IPCC, 2007). Elevated temperatures affect a range of biological processes, such as metabolic rate (Brockington and Clarke, 2001; Ganser et al., 2015), fecundity (Byrne and Przeslawski, 2013; Byrne et al., 2010), larval dispersal (O'Connor et al., 2007) and reproduction (Li et al., 2007; Tropea et al., 2015), as well as affecting the immune system, thereby decreasing disease resistance (Green et al., 2014; Hooper et al., 2014; Yu et al., 2009) and survival (Poloczanska et al., 2007). Changes in water temperature outside their optimal range will result in physiological stress for aquatic organisms. Ultimately, temperatures beyond the tolerable range will reduce the ability of an animal to function and survive (Lannig et al., 2006; Pörtner et al.,

2007; Somero, 2009). An understanding of organism's thermal tolerance is, therefore, an important step in determining possible vulnerability to ocean warming.

There are two broad categories of methods for determining the thermal tolerance of organisms; static and dynamic methods (Lutterschmidt and Hutchison, 1997; Vinagre et al., 2015). In static methods, different constant temperatures are applied in separate treatments (Terblanche et al., 2007). In dynamic methods the temperature is changed gradually or in step-wise fashion in each treatment. In both cases the end point is reached when the organisms show symptoms of having reached physiological failure, such as loss of response to a stimulus or loss of coordinated movements (Cameron et al., 2012; Diaz et al., 2013; Salas et al., 2014). The upper temperature extreme at which such symptoms occur is called Critical Thermal Maximum (CTMax) (Vinagre et al., 2015), or heat coma temperature (Clarke et al., 2000b; McMahon and Payne, 1980).

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Thermal tolerance in aquatic animals can be explained by the ability to obtain and supply sufficient oxygen to support aerobic metabolism in all tissues, which explains why other factors (such as pH or salinity) that change either the demand for, or availability of oxygen can affect the thermal tolerance of aquatic animals (Pörtner et al., 2000).

The dynamic method is more frequently used to assess CT_{Max}, as it is a simple procedure, experiments are faster and more comparable to naturally fluctuating environmental conditions (Lutterschmidt and Hutchison, 1997; Mora and Maya, 2006). However, one source of variation in the outcomes obtained using the dynamic method is how quickly the temperature is increased during the experiment. Slower temperature increments with a longer exposure may allow greater opportunity for acclimation, thereby increasing CT_{Max}. Alternatively, longer exposure times may allow more time for a physiological response to the cumulative amount of stress experienced at each increment, thus lowering the apparent upper limit (Mora and Maya, 2006; Rezende et al., 2011). Because the response times of most marine invertebrates are unknown, it may be appropriate to assess CT_{Max} under different temperature increment regimes (Rezende et al., 2014). In the intertidal zone of the subtropics water temperatures in shallow rockpools can fluctuate by more than 10 °C over a tidal cycle (Chan, 2000; Lathlean et al., 2011), so a CT_{Max} based on rapid (1 °C/30 min) warming can be important in determining tolerance of short term changes. Average seasonal sea water temperatures in northern New South Wales vary by around 5 °C (Malcolm et al., 2011), but can also vary in the short term by similar amounts. For example Baronio and Bucher (2008) observed fluctuations of water temperatures in this region of up to 5 °C over six hours and daily fluctuations of 1–2 °C are common (Lathlean et al., 2011). Therefore, CT_{Max} determined by a slower warming rate such as 1 °C/12 h) would mimic the rate of some natural changes in the shallow subtidal and deep rock pools.

CT_{Max} has been used to establish the thermal limits of aquatic and non-aquatic organisms, including molluscs, fishes, crustaceans, amphibians and insects (Beitinger et al., 2000; Dallas and Rivers-Moore, 2012; Diaz et al., 2011; Hopkin et al., 2006; Madeira et al., 2012; Terblanche et al., 2007; Vinagre et al., 2015). Several studies have specifically measured the CT_{Max} for marine gastropods in the Haliotidae (abalone) family (Hecht, 1994; Gilroy and Edwards, 1998; Diaz et al., 2006). Two previous studies have examined CT_{Max} and preferred temperatures in the turbinid snails, *Megastrea undosa* (Diaz et al., 2011) and *Megathura crenulata* (Diaz et al., 2013). However, these studies have mostly applied a single rate of warming in the experiments. Further studies of CT_{Max} are important to provide information on the potential vulnerability of commercially important fisheries species that may be impacted by global warming.

The other aspect of an animal's thermal tolerance that should be studied in conjunction with its extreme tolerable limits is the extent to which behavioural regulation of temperature can be used to compensate for ambient changes. Mobile poikilothermic animals can actively move into cooler habitats, such as deeper water or shaded areas in shallow water when water temperature rises (Munoz et al., 2005; Re et al., 2013). This behaviour of seeking out the preferred temperature is often referred to as behavioural thermal regulation (Reynolds and Casterlin, 1979). It has been suggested that the best way to demonstrate the preferred temperature of organisms is the use of laboratory gradient studies (Casterlin and Reynolds, 1980). In laboratory studies, preferred temperature can be determined from the temperature at which the organisms spends most of their time within a thermal gradient (Reynolds and Casterlin, 1979). The range of the selected temperature or 'tolerance window' is expected to represent the most appropriate ambient temperature for the organisms to maintain physiological function at maximum aerobic efficiency (Huey, 1991; Madeira et al., 2012; Pörtner, 2010; Tepler et al., 2011). A number of researchers have reported the thermal preferences of marine gastropods (Table 1), and, with the notable exception of the nassariid *Ilyanassa trivittata*, in general those from warmer climates have

higher preferred temperatures. There have only been a few studies in this regard on species in sub-tropical Australia.

South eastern Australia is one of the regions where ocean warming is predicted to increase at more than three times the global average (Hobday and Pecl, 2013). Therefore, in order to predict and monitor the ecological consequences of such changes it is important to determine the optimal range and thermal tolerance for potentially vulnerable and economically important species from this hotspot region. Turban snails (family Turbinidae) are marine gastropods, many of which are commercially or recreationally harvested around the world (Andréfouët et al., 2014; Chen et al., 2004; Mason et al., 2014; Saito and Aono, 2014; Taniguchi and Rogers-Bennett, 2001). The commercial turban fishery in New South Wales is a small-scale fishery, with total landings of 7 t annually (Rowling et al., 2010).

On the east coast of Australia two species of temperate turbinids, *Lunella undulata* and *Turbo militaris* are commonly found on intertidal and shallow subtidal reefs (Rowling et al., 2010). *L. undulata* has a distribution centred on the warm-temperate regions with subtropical conditions in the northern limits of its range, whilst *T. militaris* has a more restricted distribution not extending as far south (Fig. 1). The boundary between tropical and subtropical fauna in northern New South Wales is predicted to be a region of high sensitivity to climate change with higher than global average temperature rises and many organisms near their thermal range limits (Beger et al., 2011; Hobday et al., 2006). The aim of this study was to assess the Critical Thermal Maximum and preferred temperature for these two species of turban snails near their northern limit of distribution in NSW, Australia.

2. Materials and methods

2.1. Samples collection and acclimatisation of turban snails

All samples were collected by hand from intertidal reefs by wading at low tide (NSW Fisheries permit numbers P13/0002-1.0 and F89/1171-6.0). *L. undulata* (120 individuals with an average shell height of 2.76 ± 0.62 cm) were collected from Evans Head, Ballina, New South Wales, Australia (29°08'06.2''S, 153°27'00.0''E) in June 2013 (austral winter) and *T. militaris* (75 individuals with an average size of 8.11 ± 0.93 cm) from Woody Head, New South Wales, Australia (29°21'31.6''S, 153°21'45.6''E) in August 2013. The water temperature at the time of capture was 17 °C for *L. undulata* and 21 °C for *T. militaris*. Additional snails were collected from the same locations for the temperature preference experiments: *L. undulata* in January 2014 (austral summer, when water temperature was 23 °C) and *T. militaris* in October 2014 (austral spring, when water temperature was 22 °C). The annual range of seawater temperatures recorded in this area is from 16 °C to 27 °C (Malcolm et al., 2011). The snails were transported to Southern Cross University, Lismore in buckets with seawater and aeration within two hours of collection.

The turban snails were maintained in a flow-through water system tank of 200 L for a week to acclimatise to the laboratory conditions. The acclimatisation tank was connected to a filter tank, equipped with bio-balls and pump (Resun King 3 AF, Fountain Pump) for water recirculation. During the acclimatisation period, conditions for both species were 36–38 ppt salinity and pH 8.0–8.2. The acclimatisation temperature was the same as that measured at the point of capture. Pilot work comparing one and three-week acclimatisation periods showed no difference in CT_{Max} results, so the shorter period was considered as sufficient for the main experiment. Both species were fed macroalgae *ad libitum*, collected from the same intertidal reefs, and high feeding rates were indicative of low stress conditions. The photoperiod was maintained at a 12–12 h light–dark cycle.

2.2. CT_{Max} experiments

In order to determine the CT_{Max}, snails were divided equally

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